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Are forest management practices to improve carbon balance compatible with maintaining bird diversity under climate change? A case study in Eastern North America

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Abstract

The combination of climate change and anthropogenic disturbance significantly impacts forest bird assemblages. Assessing the cumulative effects of forest management and climate change on biodiversity and ecosystem services, including carbon sequestration and storage and provisioning of wood products is key to informing forest management and conservation decision making. Specifically, we projected changes in forest composition and structure according to various forest management strategies under a changing climate using LANDIS-II for two case study areas of Quebec (Canada): a hemiboreal (Hereford Forest) and a boreal (Montmorency Forest) area. Then, we assessed projected bird assemblage changes, as well as sensitive and at-risk species. As part of an integrated assessment, we evaluated the best possible management measures aimed at preserving avian diversity and compared them with optimal options for mitigation of carbon emissions to the atmosphere. Forest management and climate change were projected to lead to significant changes in bird assemblages in both types of forest through changes in forest composition. We projected an increase in deciduous vegetation which favored species associated with mixed and deciduous stands to the detriment of species associated with older, coniferous forests. Changes were more pronounced in Hereford Forest than Montmorency Forest. In addition, Hereford's bird assemblages were mainly affected by climate change, while those in Montmorency Forest were more impacted by forest management. We estimated that 25% of Hereford and 6% of Montmorency species will be sensitive to climate change, with projected abundance changes (positive or negative) exceeding 25%. According to the simulations, a

decrease in the level of forest harvesting could benefit bird conservation and contribute to reduction of carbon emissions in the boreal forest area. Conversely, the hemiboreal forest area require trade-offs, as mitigation of carbon emissions is favored by more intensive forest management that stimulates the growth and carbon sequestration of otherwise stagnant stands.

Introduction

There is mounting evidence that the cumulative effects of climate change and anthropogenic activities can have major impacts on biodiversity and carbon balance [1–4]. Scenarios from general circulation models (GCMs) predict a temperature increase of 3 to 5˚C across Canada's boreal zone by the end of the 21st century in the absence of greenhouse gas reductions [5, 6]. Changes in temperature and precipitation are expected to increase the frequency and severity of natural disturbances, such as wildfire, drought, and insect outbreaks [5–7]. These changes are projected to alter the distribution and availability of key habitat components such as vegetation types and food resources, alter species assemblages, and lead to the establishment of species outside their previous altitudinal [8, 9] and latitudinal [10, 11] range limits. One of the most apparent changes in eastern North America is likely to be the northward expansion of temperate and hemiboreal (*sensu* Brandt [12]) forests at the expense of boreal forests [13]. These changes are projected to cause wide-ranging impacts on associated ecosystems and biodiversity, including birds [14, 15]. For instance, warmer temperatures may lead to changes in vegetation composition, favoring the expansion of more southern and temperate species while potentially reducing suitable habitat for boreal specialists. In addition, climate change can have direct effects on ecosystem functioning, including changes in photosynthetic and metabolic rates [16, 17], and altered trophic interactions [18]. It is projected that more than half of North American bird species would experience a net loss of climatically suitable habitat at the continental scale following increased anthropogenic climate [14, 15, 19]. This shifting ecological landscape sets the stage for forest management strategies to play a pivotal role in shaping the future of bird assemblages and their habitat.

Building on this ecological context, forest management strategies significantly affect bird assemblages by altering forest stand structure and composition [20–22], including forest age distributions, canopy structure, species composition, and standing dead wood [23]. Climate change and forest management can thus interact to influence bird assemblage composition and distribution by affecting environmental characteristics [24, 25]. Indeed, the distribution and abundance of many bird species are determined by the structure and composition of the vegetation that comprises their habitat [21, 26, 27]. Moreover, modeling studies have projected that many boreal and hemiboreal forest bird species may experience declines due to climate change and the intensification of forest management [24, 25, 28]. This is especially the case for habitat specialists relative to generalist species [29, 30]. Bird species are thus not equally vulnerable, due to their specific environmental and climatic requirements and their tolerance to changes [31, 32].

Projected climate-induced changes in Quebec's forest landscapes vary due to climate velocity and a climatic gradient from temperate deciduous forests in the south to boreal coniferous forests in the north [33]. Most boreal-breeding bird species might be at risk of climate-induced changes in their habitats [32]. Indeed, in the near-term, climate change is expected to increase the risk of fires and insect outbreaks in the boreal forest, while mostly decreasing the

productivity of boreal coniferous tree species [5]. As a result, pioneer deciduous tree species are projected to be much more abundant in future boreal forest landscapes while old-growth conifer stands decrease dramatically [34]. Many bird species associated with broadleaf trees or shrubs and/or mixed conifer-broadleaf forests are thus projected to gain habitat within the current boreal forest in the future [15]. In contrast, hemiboreal forests are likely to experience smaller changes in natural disturbance regimes [34, 35]. However, northward range expansions of breeding birds inhabiting this region have already been reported [36]. Consequently, it is important to consider the heterogeneous impacts of climate change and forest management on boreal and hemiboreal forests, and how they may impact species differently throughout their ranges.

Under the United Nations Framework Convention on Climate Change, Canada committed to reduce anthropogenic emissions by 40–45% below 2005 levels by 2030 and achieve net-zero emissions by 2050. Yet, the cumulative impacts of anthropogenic disturbances and climate change on forests may affect the ecosystem's ability to sequester and store carbon [35, 37]. According to current estimates, Canada's forest sector, ecosystems and harvested wood products included, switched from being a net sink of greenhouse gases until 2001 (with exceptions during years of intense fire activity like 1995 and 1998) to a persistent net source in 2002 [38, 39]. Both climate-driven increases in natural disturbance and forest management have reduced the capability of Canada's forests to serve as a net sink in the last decades [38, 39]. Considerable uncertainty remains [40] and, the best strategy for managing carbon balance may vary among forest landscapes [41]. For instance, net carbon balance may be improved by accumulating larger carbon stocks at the ecosystem level through longer harvest rotations or conservation in some areas [41–43]. In contrast, increasing silviculture and harvest rates so that more carbon can be transferred to wood products that can be used to substitute non-renewable products [44, 45] may yield better results in other areas. Landscape characteristics that can be used as initial conditions for simulation models, such as age structure [46], baseline net ecosystem productivity [41], management system (e.g., clearcutting vs partial harvesting [41], disturbance regime [47], sensitivity to climate change [34], and substitution markets [48]), may strongly influence projected outcomes.

In this context and the realm of conservation science, ecological forecasting stands as a pivotal tool for anticipating the impacts of environmental change and guiding management decisions [49, 50]. Our study aligns with this emerging field by integrating a spatially explicit forest landscape model that consider interactions between climate and land-use changes with species distribution models to predict trends of avian diversity under shifting climate conditions and forest management practices. By coupling landscape-level vegetation changes with species-specific distribution patterns, we aimed to provide a nuanced forecast that not only predicts changes in bird assemblages but also informs management interventions to mitigate carbon emissions while preserving bird diversity. Such integrated modeling efforts are crucial for advancing the science of ecological forecasting and developing comprehensive tools that can simultaneously consider multiple variables to address the complex challenges posed by climate change [51, 52].

In a previous study, Moreau et al. [41] examined the cumulative effects of forest management and climate change on carbon dynamics to find optimal solutions for the carbon budget (i.e., sequestration and storage in ecosystems and wood products and market displacement of non-renewable, fossil-based products); management scenarios were tested that increased or decreased harvest levels and used different harvesting practices (i.e., clearcut harvest vs partial cut and longer or shorter rotations between harvests). In this study, we build on these previous analyses to evaluate management measures for sequestrating carbon or replacing fossil fuels with biofuels while maintaining avian diversity on the landscape. While climate change can

influence species in many ways, our study focused on the consequences of habitat change. More specifically, our objectives were to 1) identify the cumulative and specific impacts of climate change and forest management on bird assemblages and identify species most sensitive to changes, 2) integrate projected shifts in bird assemblages with carbon emission mitigation strategies explored in Moreau et al. [41] across diverse management and climate change scenarios, 3) examine if two distinct forest landscapes exhibit similar or divergent responses, and 4) investigate the best management measures to preserve avian diversity and mitigate carbon emissions.

Methods

1. Study areas

We focused on two study areas: Montmorency Forest within the boreal region and Hereford Forest within the hemiboreal region (Fig 1).

Montmorency Forest (37,050 ha) is located in the Boreal shield ecozone. The most common stand types are typical of the balsam fir (*Abies balsamea*) and white birch (*Betula papyrifera*) bioclimatic domain of the boreal forest, with a component of white spruce (*Picea glauca*), black spruce (*Picea mariana*), and trembling aspen (*Populus tremuloides*). The main natural disturbances are insect outbreaks, mostly eastern spruce budworm outbreaks (*Choristoneura fumiferana*), and windthrow [53] Montmorency Forest has a long history of forest management. Clearcut harvesting followed by natural regeneration and, to a lesser extent, partial harvesting that maintains a continuous forest cover are conducted in Montmorency Forest.

Hereford Forest (5,669 ha) is located in the Atlantic Maritime ecozone in the hemiboreal subzone, which is considered to be part of the temperate zone but transitional to the boreal ([12], Fig 1). The vegetation is characteristic of the hemiboreal sugar maple (*Acer saccharum*) and yellow birch (*Betula alleghaniensis*) bioclimatic domain, which is mainly composed of those two species mixed with intolerant hardwoods, balsam fir and red spruce (*Picea rubens*).
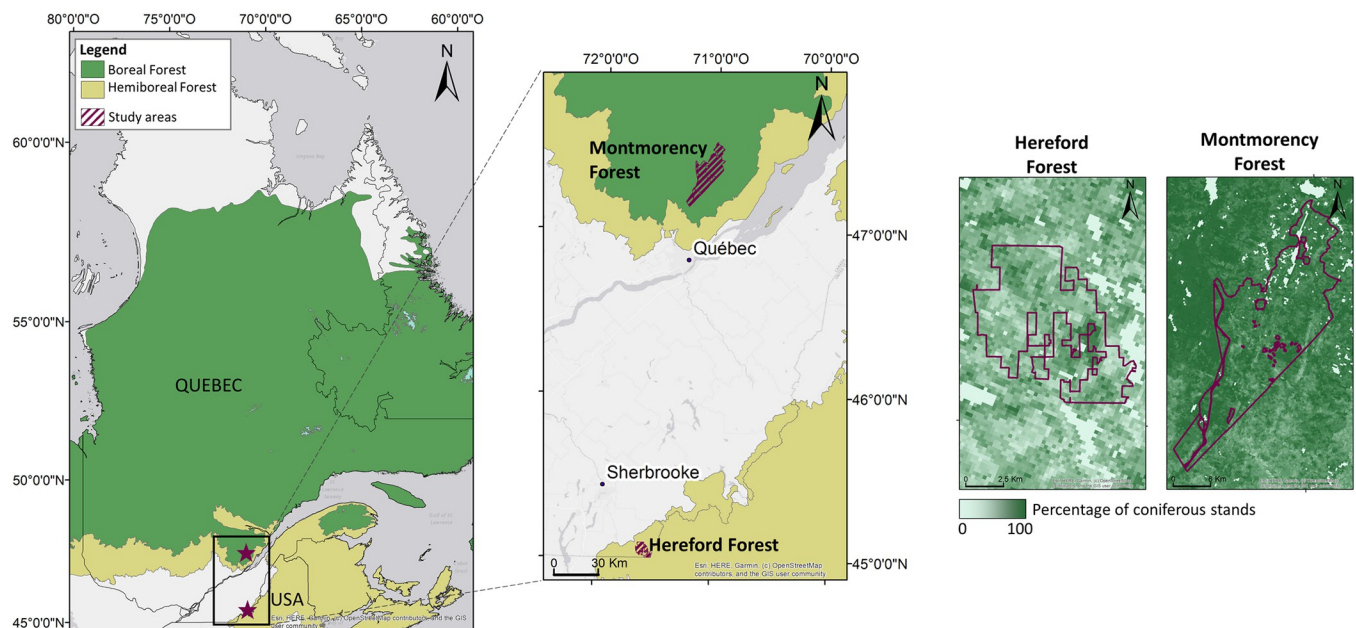

Fig 1. Location of the two study areas (hashed) and the North American boreal zones in Canada [12]. The percentage of coniferous is shown with a gradation of greens. Sources of the basemap: Esri, HERE, Garmin, OpenStreetMap contributors, and the GIS User Community [57].

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The main natural disturbances are small windthrow and insect outbreaks [54]. The region shows centuries of human occupation related to urban and agricultural developments and forest management following to Euro-American settlement resulting in forest fragmentation and a scarcity of old-growth forests. Hereford Forest has been characterized by high-grading selection cutting, which greatly shaped the forest landscapes present today. Before 1850, Hereford Forest was mainly composed of mature forest (i.e., > 70 years old), while 98% of the current forest is < 50 years old. Current forest management practices in Hereford Forest include retaining small patches of partial cuts (1–10 ha per patch) and conservation areas (ca 10% of the territory).

Wildfires are not a major natural disturbance in these areas (e.g., mean fire return interval of more than 1000 years) and are not projected to become major in the near future [55, 56]. Forest composition in 2020 for the two types of forests is detailed in S1–S3 Figs.

2. Spatially explicit forest simulation model

a. Climate scenarios. Future climate projections for the 100 years of simulation were based on three different global warming trajectories:

- A baseline scenario with no climate change, which corresponds to a projection of current (1981–2010) climate conditions, with no change in the 100 years of simulation.

- Two radiative forcing scenarios: Representative Concentration Pathway (RCP) 4.5 and 8.5 [58].

Of the two pathways, the RCP 4.5 scenario is more optimistic with a projected increase in future mean annual temperatures of about 3˚C. In contrast, the RCP 8.5 scenario is more pessimistic with a predicted increase of 7.5˚C in the study area by 2100 (compared with 2000), while average precipitation is projected to increase between 7% and 10% under RCP 8.5 and RCP 4.5 respectively [59]. We obtained future climate projections from the Canadian Earth System Model version 2 (CanESM2) ran under both scenarios [60], downloaded from the Climate Model Intercomparison Project Phase 5 (CMIP5) archives of the World Climate Research Program (WCRP) and Ouranos [61]. CanESM2 data were biased-corrected for the period 1961–1990 to incorporate data from McKenney et al. [62], particularly for temperature values and precipitation ratios. Climate change (CC) scenarios were produced using data from climate station records [62]. The ANUSPLIN method was used to downscale climate projection to a 10-km resolution [62].

b. Forest landscapes simulations with LANDIS-II. We used LANDIS-II v6 [63] to simulate the spatial dynamics of forest ecosystems, focusing on the interaction of ecological processes at stand and landscape scales [59]. This model integrates various ecological processes through distinct extensions, tailored to specific research questions and complexity levels. Our simulations incorporated the effects of climate change on tree growth and establishment, as well as the frequency and severity of natural disturbances. We used the LANDIS-II Biomass Succession extension v3.2 to project forest succession and bird habitats, with parameters derived from PICUS v1.5 [64, 65] and climate data from CanESM2. Simulations ran for 80 years from 2020, with a 10-year timestep and 250-m resolution. For a detailed description of the simulation setup and parameterization, refer to the Supporting Information–S1 Text.

c. Natural disturbances. We simulated spruce budworm outbreaks and windthrow as natural disturbances. Both disturbances historically had major impacts on forest landscapes in these areas [66, 67]. Spruce budworm (SBW) outbreaks were simulated using the Budworm Biological Disturbance Agent (BDA) extension (v3.0; [68]), specifically designed to simulate host tree mortality following insect outbreaks. SBW outbreaks were calibrated using Boulanger

et al. [34] parameters and were set to the maximum severity and to recur every 40 years (2030 and 2070) in accordance with the historical regional outbreak cycle [67]. Host species included, ranking from the most to the least vulnerable, balsam fir, white spruce, red spruce and black spruce. Forest composition resulting from spruce budworm outbreaks (i.e., the increase in the proportion of mixed stands) was tracked. Windthrows were simulated using the Base Wind extension [69]. This natural disturbance was set as a background disturbance set to occur most often in older stands regardless of species composition and according to a 2500-year cycle. Although these disturbances were not impacted by climate conditions *per se*, their severity was a function of stand age and/or forest composition which themselves are strongly function of climate change.

d. Forest management scenarios. To determine the impact of forest management for each of the two areas, several management scenarios were defined based on inputs from local forest managers, reflecting realistic actions for their respective territories. More specifically, as part of a coordinated project with Moreau et al. [41], we compared four different possible forest management scenarios that differed in terms of wood volume harvested. The simulated forest management scenarios reflected realistic actions for their respective areas, and were classified as 1) no harvest (no harvesting was performed), 2) business-as-usual (BaU, current forest management strategy) 3) conservation (i.e., reduction of management intensity and volume harvested relative to the BaU), and 4) intensification (increase of management intensity and volume harvested relative to the BaU). Forest management scenarios were modulated according to local characteristics and associated silvicultural practices (Table 1). For

Table 1. Forest management scenarios for a) Montmorency (MF) and b) Hereford (HF) Forests. The reference scenario is Business–as–usual.

Montmorency Forest

Scenarios	Silvicultural practices	Targeted harvest rate (% area)
No harvest	Natural succession	0%
Business-as-usual (BaU)—Reference	Partial Cut (33% / 30 years) Clear Cut with Age (23–35% / 50 years)	PC: 0.160% / year CPRS: 0.637% / year
Conservation—Reduced harvesting or increased rotation time	Partial Cut (33% / 30 years) Clear Cut with Age (30–40% / 70 years)	PC: 0.509% / year CPRS: 0.273% / year
Intensive—Increased harvesting	Clear Cut with Age (30–40% / 50 years)	CPRS: 0.785% / year

Hereford Forest

Scenarios	Zoning	Silvicultural practices	Targeted harvest rate
No harvest	The entire area	Natural succession	0%
Business-as-usual (BaU)—Reference	Conservation area	Natural succession	0%
	Multiple-use area	Partial Cut (30–35% / 15 years)	PC: 3.7% / year
Conservation—Reduced harvesting or increased rotation time	The entire area	Partial Cut (30–35% / 25–30 years)	PC: 3.62% / year
Intensive—Increased harvesting	The entire area	Partial Cut (30–35% / 12–15 years)	PC: 7.4% / year

Note: PC (Montmorency Forest): Partial cut with permanent cover, cutting X% every Y years; PC (Hereford Forest): Partial cut with permanent cover if the oldest cohort is at least 50 years old; CPRS: clear cut if the oldest cohort is at least 50 years old. Details of the forest management framework can be found in Moreau et al. [41].

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Montmorency Forest, intensity of forest management and harvest level varied both by harvested volume (increased or decreased harvested volume) and by type of cut (proportion of clearcut vs. partial cut). For Hereford Forest, the intensity of management and harvest level differed between scenarios according to the rotation time between two partial cuts (either shorter or longer) and by the absence or presence of a conservation area (Table 1). For both areas, partial cutting of forest stands did not reset stand age to 0 (contrary to clearcut), as age is based on the oldest tree cohort.

The different forest management scenarios were simulated using the Biomass Harvest extension (v3.0; [70]). Each cell was considered as a stand belonging to a given forest management unit (FMU) in which specific prescriptions were set to occur at specific rates over the FMU. Each prescription is defined according to various stand- and FMU-level parameters including the proportion of biomass harvested at each harvest event, harvested patch size, minimum stand age to be harvested, which cohort should be harvested and the proportion of the FMU that should be harvested according to this prescription per timestep. Harvest rates were held constant throughout the simulations unless not enough stands qualified for harvest. In this latter case, harvest proceeded until no more stands were available.

e. Simulation design.   Each combination of climate and forest management scenarios was replicated 5 times, to consider the effects of stochastic parameters [71]. For the next steps of the analysis, we used landscapes resulting from LANDIS-II model for the years 2050 and 2100.

3. Bird species models

In order to model bird assemblages in each of the two study areas, we built species-specific predictive abundance models using species and sampling event-specific detectability offsets using the "QPAD" approach ($E[Y] = Q \times P \times A \times D$ where perceptibility [Q], availability [P], area [A] and density [D]) according to methods described in Sólymos et al. [72]. This approach accounts for variation in sampling protocols and the effects of covariate on detectability. By incorporating offsets in the generalized linear models, this approach enabled to standardize the estimates and reflect density (number of singing individuals per hectare) within different forest landscapes. Bird observations were retrieved from the Boreal Avian Modeling Project database (BAM; borealbirds.ca) which includes data from a variety of sources including the volunteer Breeding Bird Survey (BBS; pwrc.usgs.gov/bbs) and the Québec breeding bird atlas (atlas-oiseaux.qc.ca) with various institutional and individual contributors. We retained only forest landbird species known as common breeders in each area based on the seasonal histograms of ebird sightings (ebird.org), resulting in a total of 51 species for Montmorency Forest and 45 species for Hereford Forest (S1 Table). For each of these species, we modeled density (males/ha) as a function of different vegetation and landscape variables using Boosted Regression Trees (BRT; [73]) with a Poisson distribution. We capped the number of trees at 10,000, and used a learning rate of 0.001, bag fraction of 0.5, and interaction depth of 3, as recommended by Elith et al. [74] and consistent with Stralberg et al. [75]. We used 47 variables, characterizing the forest structure and composition at local and landscape scales (S2 Table). In order to be compatible with LANDIS-II species biomass and stand age outputs, these vegetation variables were based on vegetation models derived from the Canadian National Forest Inventory [76]. The covariates used for the bird model fitting were either: (i) assumed static (i.e., varied in space, but did not change in LANDIS-II simulations) over the simulated period (e.g., water bodies, wetland); (ii) dynamic and allowed to change between simulations and time steps in LANDIS-II simulations (tree species, biomass, age, and climate covariates). Variables included the proportion of each cell dominated by different tree species in each region; total live above-ground vegetation biomass in each cell and stand age. We used the compound

topographic index (CTI) as a measure of soil moisture based on slope and catchment area: areas with low CTI values have small catchment areas with steep slopes [77, 78]. As suggested by Chandler and Hepinstall-Cymerman [79], we quantified variables at two spatial extents: the original value assigned to each 250-m cell ("local effect") and mean values at landscape scale based on a Gaussian filter with sigma = 750 m (*focalweight* function in "raster" package [80], in R). We used the *gbm.step* function in the "dismo" package [81] in R to build and predict the models. We used cross-validation correlation statistics (S1 Table) as indicators of model performance and summed variable importance scores for vegetation and climate predictors to assess the relative importance of vegetation and topography in each species' model (S3 Table). This allowed to track population trends for each bird species, as well as for bird assemblages. The classification of bird species according to their primary habitat associations was achieved by integrating predictions of densities with insights from specialists in the field. Consequently, the composition of bird assemblages was established based on forest cover and age (i.e., habitat) classes (S1 Table).

4. Data analyses

a. Bird abundance.   We used the predicted density values from BRT models to estimate the relative abundance of each bird species for all LANDIS-II simulations at each time step. The results of the five replicates were averaged for each of the scenario.

b. Trends in bird abundance: Effects of climate change and forest management.   To examine the pattern of bird abundance according to climate change and forest management scenarios, we conducted a non-metric multidimensional scaling (NMDS) ordination with a Bray-Curtis distance matrix using the function *metaMDS* in the "vegan" package [82] in R. The vectors of climate and forest management scenarios were fitted to the ordination using the *envfit* function of the "vegan" package in R. Each vector was independently fitted to the underlying ordination. The significance of the fit of each vector to the ordination was assessed with a Monte-Carlo analysis of 999 permutations.

c. Impacts of climate change and forest management on bird assemblages in boreal and hemiboreal forests.   To have an overall overview of the cumulative impact of climate change and forest management on projected bird assemblages, we quantified bird alpha diversity (Shannon diversity) of each study area using the package 'vegan' [82] in R.

Then, the cumulative impact of both drivers of change on projected bird abundance was calculated as the percent change in projected bird abundance relative to the abundance under BaU management and baseline climate scenario (hereafter referred as the "reference scenario") using the equation as in Cadieux et al. [25]:

$$\text{Percent change} = ((\text{ProjAbund}_t/\text{RefAbund}_t)-1) \times 100 \qquad (Eq1)$$

where RefAbund$_t$ is the abundance of a bird species under the reference scenario, ProjAbund$_t$ is the projected abundance of the same species for a given combination of scenarios (Forest management × climate) at a given future time and t is the time in years. We used this method to assess the cumulative effects of climate change and forest management while controlling forest succession [24].

We conducted this analysis on bird assemblages in addition to individual species to understand the general trend of the cumulative impacts of climate change and forest management on multiple species of birds sharing similar habitat requirement in boreal and hemiboreal forests and how their response may differ spatially. The cumulative impacts of forest management and climate change are considered important for bird assemblages when an assemblage shows

an increase in abundance of more than 10% or a decrease in abundance of less than 10% of the population compared to the reference scenario.

The relative importance of each driver of change (climate change and forest management) was assessed by estimating the variance of bird abundance explained using omega-squared values (ω^2). Following a two-way factorial ANOVA, where each driver of change was considered as a factor, we calculated ω^2 for each driver of change, at each time step, as in Cadieux et al. [25]:

$$\omega^2 = (\text{SS}_{\text{effect}} - (\text{df}_{\text{effect}} \times \text{MS}_{\text{error}}))/(\text{MS}_{\text{error}} + \text{SS}_{\text{tot}}) \qquad (\text{Eq2})$$

where SS_{effect} is the sum of squares related to the driver of change (the effect), df_{effect} is the degree of freedom of the effect, MS_{error} is the mean square of the error, and SS_{tot} is the total sum of squares. ANOVA and ω^2 calculations were performed separately for each RCP scenario.

d. Species at risk and sensitive species.   Three forest bird species (i.e., Canada Warbler (*Cardellina canadensis*), Rusty Blackbird (*Euphagus carolinus*), and Eastern Wood-pewee (*Contopus virens*)) are considered at risk in our study based on their provincial and/or federal status [83].

Species were considered sensitive if they demonstrated at least a 25% projected increase or decrease compared to the reference population [25].

e. Dual-criteria approach.   To assess management measures that best address both criteria (i.e., preservation of avian diversity and mitigation of carbon emissions), we compared our results with those from Moreau et al. [41], which evaluated the same forest management scenarios with respect to carbon emission mitigation potential within Hereford and Montmorency Forests. That study considered carbon sequestration and emissions in forest ecosystems as influenced by management scenarios, carbon emissions from degradation of harvested wood products during their service life and in landfills, and the avoided emissions (recorded as carbon sequestration) caused by substitution, by wood products, of non-renewable, fossil-based materials and energy sources on markets. The mitigation potential of a given management scenario was calculated as the difference between the total emissions/sequestrations of this scenario (Ecosystems + Products + Substitution) and that of the Business-as-usual (BaU) management scenario; a positive value indicates that the alternative scenario increases emissions to the atmosphere relative to the BaU, while a negative value indicates that it decreases emissions/increases sequestration. We thus compared forest management scenarios that are projected to be the best to maintain bird assemblages (i.e., with a small percent change compared with the reference scenario) with scenarios that best maximize the emission mitigation potential (i.e., enhance net sequestration) relative to the BaU.

All analyses were conducted in program R version 4.2.2 [84].

Results

1. Cumulative impacts of climate change and forest management on tree species biomass

1.1. Boreal forest–Montmorency.   General trends in forest compositional changes over the simulated period were directly linked to forest management (S1 Fig). An increase in the level of forest harvesting was associated with a decrease in mean aboveground biomass (S1 Fig) and a decrease in mean stand age (S2 Fig). The proportion of trembling aspen increased with the level of forest harvesting at the expense of white spruce and black spruce (S3 Fig). For a given forest management scenario, results also suggested that forest composition was projected to have little variation between the three climate scenarios (S3 Fig).

1.2. Hemiboreal forest–Hereford. General trends in forest compositional changes over the simulated period were linked to both forest management and climate change (S1 Fig). An increase in the level of forest harvesting was associated with a decrease in mean aboveground biomass (S1 Fig). Climate change and forest management did not influence the mean stand age, mostly due to partial cutting management, which was projected to increase linearly over time (S2 Fig). The proportion of sugar maple was projected to increase with the level of forest harvesting, especially under baseline climate scenarios, at the expense of balsam fir and red maple (*Acer rubrum*; S3 Fig). In addition, the proportion of American beech (*Fagus grandifolia*) and red spruce were projected to increase with the severity of climate change (S3 Fig). However, the proportion of sugar maple was projected to decrease with the severity of climate change (S3 Fig).

2. Projected bird assemblage changes

2.1. Trends in bird abundance: Effects of climate change and forest management. Stable NMDS ordinations of predicted change in bird abundance under cumulative effects of climate change and forest management were obtained after 29 iterations of 20 tries with a final stress of 0.08 in Hereford Forest, and after 110 iterations of 20 tries with a final stress of 0.07 in Montmorency Forest. These low stress values suggest that the ordinations were not arbitrary and that the plots provide a realistic portrait of the distance between change in bird abundance depending on climate change and forest management scenarios. The magnitude of bird abundance change was correlated with both climate change forcing scenarios and the intensity of forest management over time, with the largest value in 2100 (Fig 2). There was a stark change in bird abundance between the baseline climate scenario and both moderate (RCP 4.5) and high (RCP 8.5) climate scenarios across forest management scenarios for both study areas, suggesting that important changes in bird abundance are projected to occur under a warming climate. In both Montmorency and Hereford Forests, the NMDS analysis revealed a consistent gradient in the impact on bird abundance across different forest management scenarios (NMDS1, Fig 2). This gradient was observed in the order of Intensive > BaU > Conservation > No harvest scenarios. Notably, the Montmorency Forest exhibited a more pronounced change in bird abundance across these scenarios compared to Hereford Forest.

Close associations between bird abundance changes and several forest characteristics were predicted (Fig 2). In Hereford Forest, bird abundance was mostly linked to the projected proportion of balsam fir ($R^2 = 0.70$, $P < 0.01$). In Montmorency Forest, bird abundance was mostly related to the projected proportion of white spruce ($R^2 = 0.83$, $P < 0.01$) and black spruce ($R^2 = 0.75$, $P < 0.01$).

The Shannon diversity index, indicative of an overall bird abundance changes, exhibited distinct temporal and spatial patterns within Hereford and Montmorency Forests. By 2100, projections suggest a consistently higher Shannon index in Hereford Forest across all climate and forest management scenarios compared to Montmorency Forest (Fig 3). Notably, in Hereford, the index was higher under the RCP 8.5 scenario than the baseline, contrasting with Montmorency where the reverse was observed. Climate change appeared to be the predominant driver affecting diversity in Hereford Forest, with minimal variation across management scenarios. In contrast, forest management played a more significant role in shaping diversity within Montmorency Forest.

The magnitude of projected changes in bird abundance under high climate warming (RCP 8.5) at year 2100 relative to the one simulated under baseline climate varied greatly among areas, species, habitat type associations and the level of forest harvesting (Fig 4, S5 and S6 Tables). Forest generalist species were projected to be favored by the intensification of forest
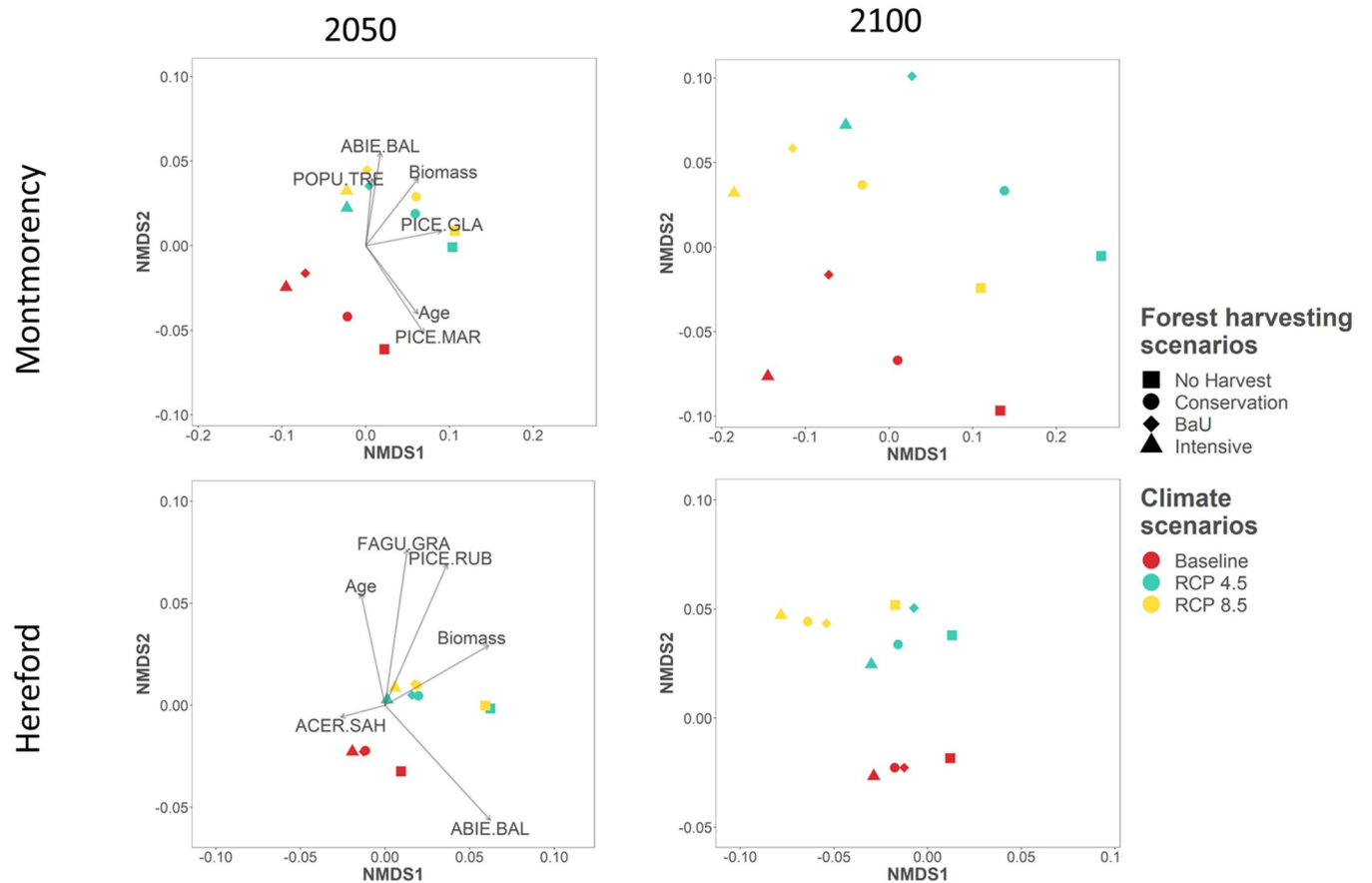
Fig 2. Non–metric multidimensional scaling (NMDS) ordination of bird abundance with the most highly correlated climate and forest management scenario variables at years 2050 (left) and 2100 (right) for Montmorency (top) and Hereford (bottom) Forests. Arrows represented forest characteristic variables Age, Biomass, the proportion of balsam fir (ABIE.BAL), white spruce (PICE.GLA), black spruce (PICE.MAR), sugar maple (ACER.SAH), American beech (FAGU. GRA), trembling aspen (POPU.TRE), and red spruce (PICE.RUB). Correlation coefficients between variables and the two axes are presented in S4 Table.

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harvesting in both forests (Fig 4 and S5 Table). However, the intensification of forest harvesting was projected to have a negative impact on birds associated with mature and coniferous stands (i.e., High percentage of change; Fig 4), especially in Hereford Forest. In Hereford Forest, most bird assemblages would be negatively impacted by forest management. In Montmorency Forest, most bird assemblages would be favored, while most had a percent change less than 10% (Fig 4 and S5 Table). In addition, the magnitude of change was projected to be generally greater at Hereford Forest than at Montmorency Forest.

2.2. Specific impacts of climate change and forest management scenarios on bird assemblages. Climate-driven ecological processes (i.e., tree growth and regeneration) had more important projected influences on Hereford Forest than Montmorency Forest bird assemblages under RCP 8.5 by 2100 (Fig 5 and S5 Table). For each study area, the importance of each driver of change (i.e., climate change and forest management) was similar between RCP 4.5 and RCP 8.5 but varied between 2050 and 2100 (S4 Fig). Indeed, in Hereford Forest, the climate-driven ecological processes were projected to have more important projected influences on bird assemblages in 2100 than in 2050; while forest management would have less impact. In contrast, in Montmorency Forest, the climate-driven ecological processes were projected to have a smaller influence on bird assemblages in 2100 than in 2050; while forest management was projected to have more impact.
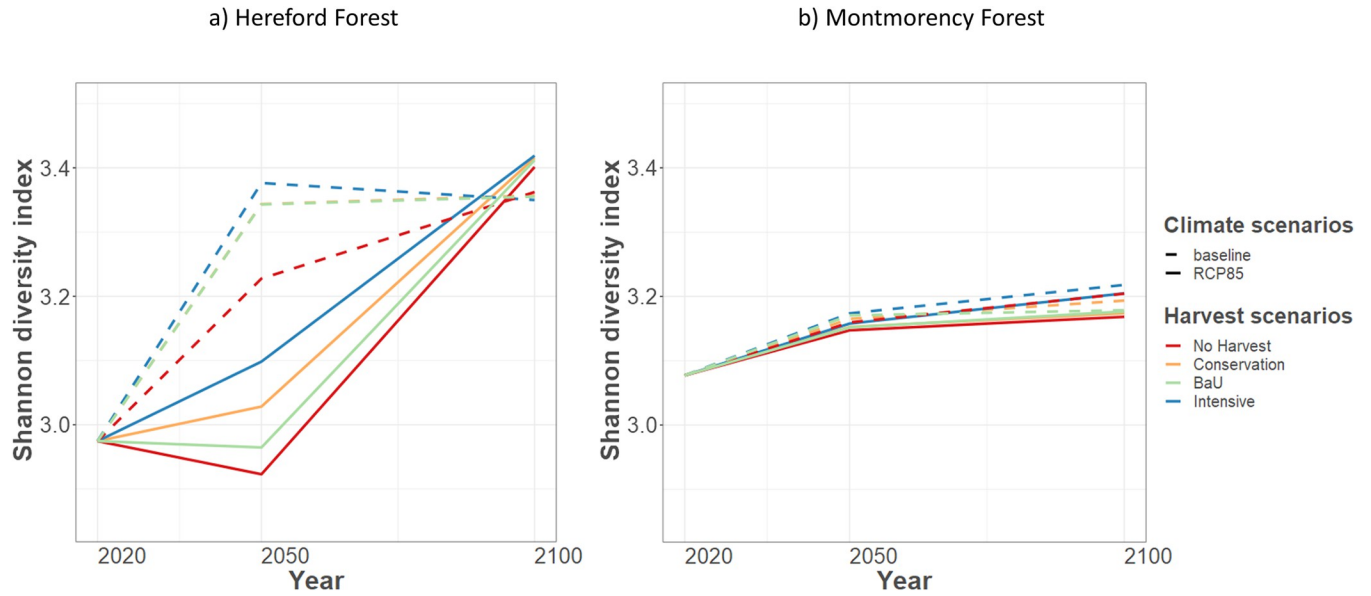
Fig 3. Impacts of forest management on Shannon diversity index in a) Hereford Forest and b) Montmorency Forest under Baseline (hatched) and RCP 8.5 (solid) climate scenarios.

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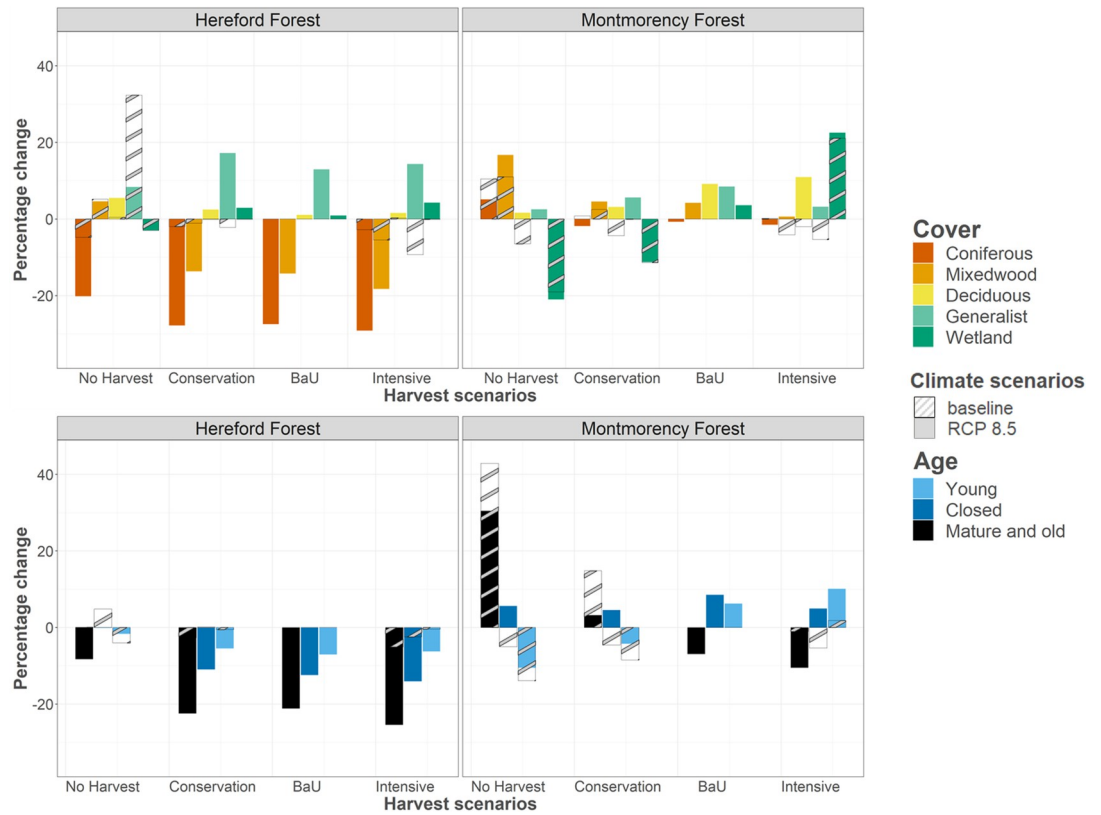
Fig 4. Density projections of bird species associated with cover types (top) and age categories (bottom) under Baseline (hatched) and RCP 8.5 (solid) climate scenarios at year 2100 for Hereford Forest and Montmorency Forest. The reference scenario is the baseline–BaU scenario.

https://doi.org/10.1371/journal.pclm.0000293.g004

Fig 5. The relative contribution of drivers of change (climate change and forest management) as values of ω^2 (mean), under RCP 8.5 at year 2100 relative to the change simulated under baseline climate.

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In Hereford Forest, compared to the reference scenario (i.e., Baseline—BaU scenario), for the most severe climate scenario (i.e., RCP 8.5) under the BaU management scenario, climate change was mostly detrimental to birds associated with 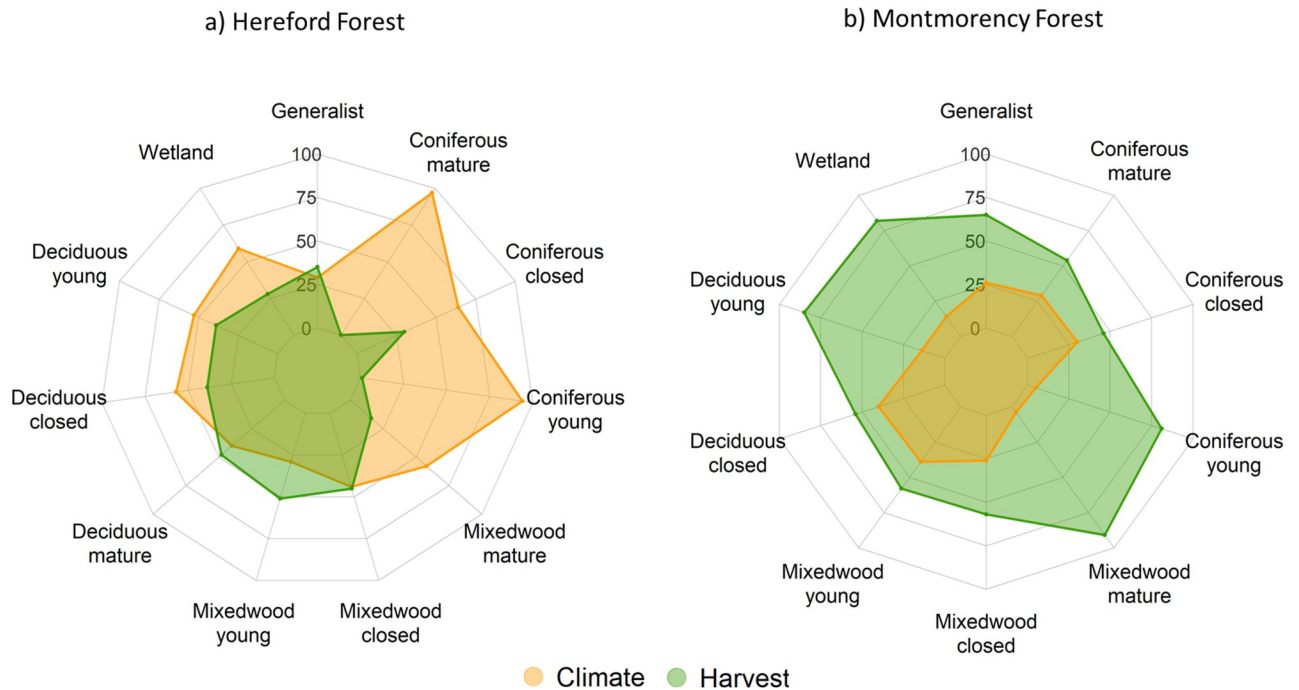closed mixedwood (Percent change = -14 ±16; mean, SD), and coniferous forests (Percent change = -24 ±15), explaining more than 44% of the decline in these bird species' abundances by 2100 (Fig 5A and S5 Table). Within bird assemblages showing strong or mixed (i.e., $|\omega^2_{harvest} - \omega^2_{Growth}| < 25\%$) effects of forest management and climate change, generalist species and young deciduous-associated bird species were predicted to increase under all forest management scenarios except 'No harvest'. In contrast, the abundance of birds associated with mature deciduous, and closed mixedwood forest stands, while also driving by mixed effects of climate change and forest management, declined for all levels of forest harvesting excepted for 'No harvest' (S5 Table).

Comparatively, in Montmorency Forest, changes in bird assemblage abundance were mostly driven by forest management, a climate-independent driver (Fig 5B). Only species associated with closed deciduous forests were projected to be affected primarily by the combined effects of climate change and forest management (Fig 5B and S6 Table). While forest management explained more than 46% of the change in all bird species' abundances by 2100 (Fig 5B), the percent change in each species was mostly < 25% (S6 Table).

Some species currently occurred in both forests, such as Blue-headed Vireo (*Vireo solitarius*), Yellow-rumped Warbler (*Setophaga coronata*), and Black-throated Green Warbler (*Setophaga virens*), species associated with closed mixedwood stands. Our analysis revealed that change in abundance of these species would be driven primarily by climate change ($\omega^2 \geq 50\%$) in Hereford Forest, while it would be driven by forest management ($\omega^2 \geq 88\%$, except for the Yellow-rumped Warbler where $\omega^2 = 33\%$) in Montmorency Forest (S6 Table). In Montmorency Forest, of the 6 species that were projected to be mostly affected by climate change by 2100 ($\omega^2 > 59\%$), 5 (e.g., American Goldfinch (*Spinus tristis*), Philadelphia Vireo (*Vireo*

philadelphicus), Canada Warbler, Blackburnian Warbler (*Setophaga fusca*), and Northern Parula (*Setophaga americana*) also in Hereford Forest (S6 Table). Moreover, our analysis revealed that change in abundance of Philadelphia Vireo, Canada warbler and American Goldfinch driven by climate change ($\omega^2 \geq 60\%$) in Montmorency Forest, while it would be driven by forest management ($\omega^2 \geq 58\%$) in Hereford Forest (S6 Table).

3. Identification of bird species sensitive to climate change and forest management

Of the 45 bird species in Hereford Forest, we identified 8 (16%) and 4 (9%) species that were projected to decline and increase in abundance, respectively, by more than 25% by 2100 for the most severe climate change scenario (RCP 8.5) under the BaU management scenario compared to the reference scenario (Fig 6 and S6 Table). Of those 12 species, the abundance of 11 species was driven by climate change ($\omega^2 > 25\%$), including two species with mixed effects (i.e., the difference between both $\omega^2 < 25\%$; S6 Table). Species that were projected to increase greatly were generalist species and bird species associated with deciduous stands (average increases of 28% and 48%, respectively). Of all increasing species in Hereford Forest, only Pine Siskin (*Spinus pinus*) also occurred in Montmorency Forest (S6 Table). Moreover, 62% of the predicted declining species (i.e., 5 species) were birds associated with closed coniferous and mixedwood stands (average decline by -39% and -33%, respectively). Except for Scarlet Tanager (*Piranga olivacea*), the other seven declining species in Hereford Forest also occurred in Montmorency Forest, but were projected to be less impacted by climate change and forest management (i.e., Percent change < -25%; S6 Table). In addition, under RCP 8.5 and the BaU management scenario, three species were projected to decline and by more than 25% and one species was projected to increase by more than 25% by 2100 compared to the reference scenario (Fig 6 and S6 Table).

In Montmorency Forest, of the 51 species, we identified one (Black-backed Woodpecker (*Picoides arcticus*), 2% of the total) and two (American Goldfinch and Philadelphia Vireo, 4% of the total) species with populations that were projected to decline or increase by more than 25% compared to the reference scenario (Fig 6 and S6 Table). Of those 3 species, all were predicted to be impacted by climate change ($\omega^2 > 25\%$). American Goldfinch and Philadelphia Vireo were predicted to increase greatly (average increase of 30%), and the declining species, Black-backed Woodpecker, was projected to decline by 39%. Black-backed Woodpecker decline was projected to be mostly driven by forest management ($\omega^2 = 60\%$). Except for this declining species, the two increasing species in Montmorency Forest also occurred in Hereford Forest, but were projected to be less impacted by climate change and forest management (i.e., Percent change < 25%; S6 Table). In addition, one species (Rusty Blackbird) was projected to decline by more than 25% and two species (Black-throated Blue Warbler (*Setophaga caerulescens*) and Canada warbler) were projected to increase by more than 25% by 2100 compared to the reference scenario (Fig 6 and S6 Table).

Interestingly, the relative influence of the drivers of change did not show similar patterns under RCP 4.5 and 8.5 for some species, such as Yellow-rumped Warbler in Hereford Forest, and American Goldfinch in Montmorency Forest (S5 Fig). For Yellow-rumped Warbler, and American Goldfinch, forest management was predicted to be more influential for a shorter period of time under RCP 4.5 compared to RCP 8.5 (S5 Fig).

4. Impacts of climate change and forest management scenarios on species at risk

The relative contribution of climate-driven ecological processes and forest management scenarios varied among species at risk, but also between simulated forests within species (Fig 6).
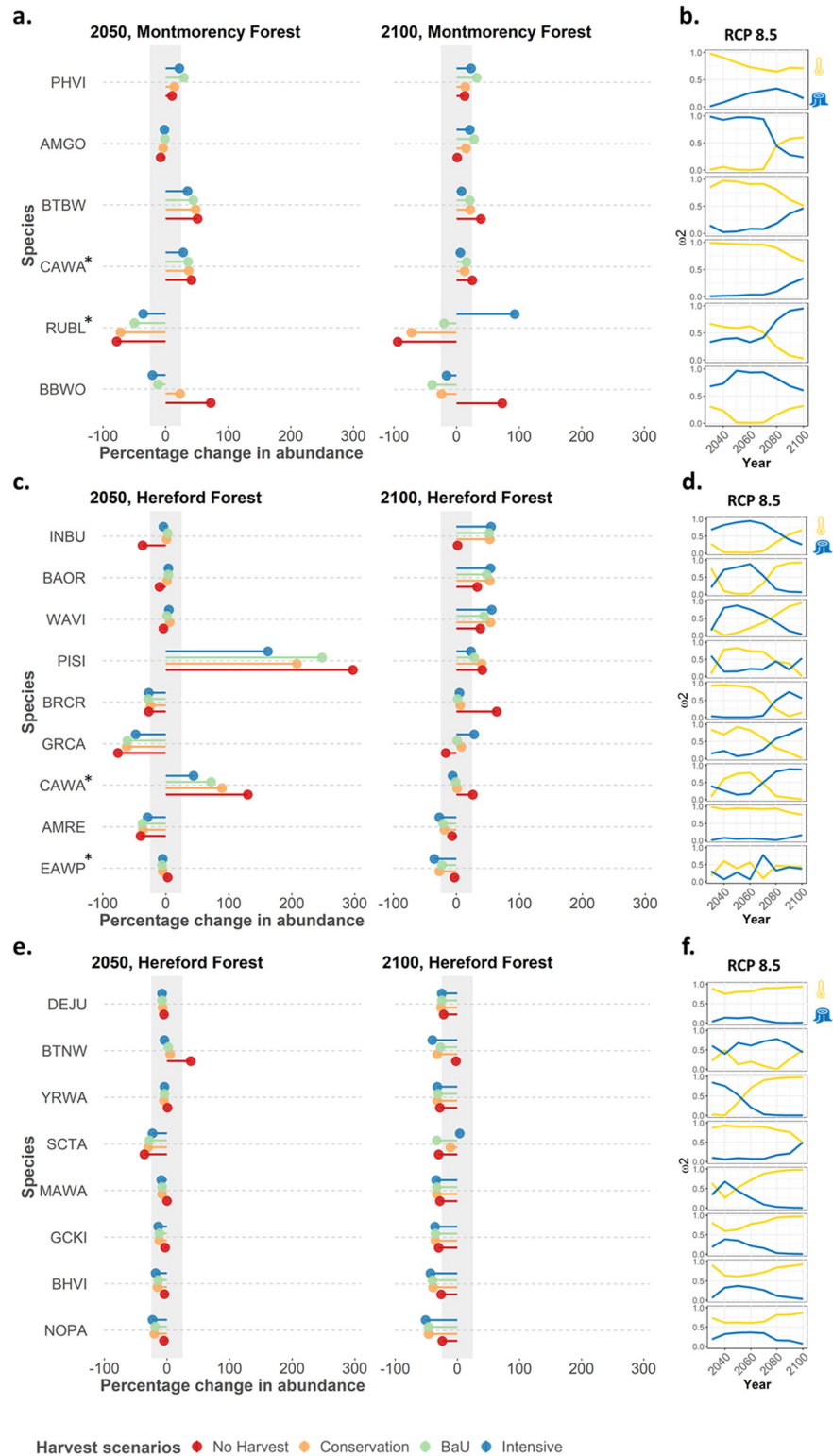
Fig 6. a, c, d) Percent change in abundance of sensitive bird species under RCP 8.5 at year 2050 and 2100 relative to the change simulated under the reference scenario (Baseline–BaU scenario) in (a) Montmorency, and (c,d) Hereford Forests; b, d, f) represent the temporal trends of the relative contribution of drivers of change (climate change and forest management) as values of ω^2 under RCP 8.5 in (b) Montmorency, and (d,f) Hereford Forests. Shaded areas represent |%change| < 25%. Species indicated with an asterisk represent species at risk. Birds represented are

Philadelphia Vireo (*Vireo philadelphicus*, PHVI), American goldfinch (*Spinus tristis*, AMGO), Black–throated Blue Warbler (*Setophaga caerulescens*, BTBW), Canada Warbler (*Cardellina canadensis*, CAWA), Rusty Blackbird (*Euphagus carolinus*, RUBL), Black–backed Woodpecker (*Picoides arcticus*, BBWO), Indigo Bunting (*Passerina cyanea*, INBU), Baltimore Oriole (*Icterus galbula*, BAOR), Warbling Vireo (*Vireo gilvus*, WAVI), Pine Siskin (*Spinus pinus*, PISI), Brown Creeper (*Certhia Americana*, BRCR), Gray Catbird (*Dumetella carolinensis*, GRCA), American redstart (*Setophaga ruticilla*, AMRE); Eastern Wood–pewee (*Contopus virens*, EAWP), Dark–eyed Junco (*Junco hyemalis*, DEJU), Black–throated Green Warbler (*Setophaga caerulescens*, BTNW), Yellow–rumped Warbler (*Setophaga coronata*, YRWA), Scarlet Tanager (*Piranga olivacea*, SCTA), Magnolia Warbler (*Setophaga magnolia*, MAWA), Golden–crowned Kinglet (*Regulus satrapa*, GCKI), Blue–headed Vireo (*Vireo solitarius*, BHVI), and Northern Parula (*Setophaga Americana*, NOPA).

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For example, in Montmorency Forest, our projections indicate that climate-driven ecological processes will predominantly influence the abundance of the Canada Warbler throughout the entire simulation period (Fig 6B). A similar trend is expected in the Hereford Forest until around 2075. However, post-2075, forest management is projected to become the more dominant influence on the Canada Warbler's abundance in Hereford Forest, where its impact is estimated to be 88% (ω^2_{2100}, Fig 6D). While the drivers of change were projected to differ among areas for Canada Warbler at the end of the century, we predicted that this species would be more or less sensitive to the vegetation changes induced by climate change and forest management depending on the period of time (Fig 6A and 6c, S6 Table). In Montmorency Forest, we predicted that Canada Warbler and Rusty Blackbird would be more sensitive to climate change and forest management in 2050, compared to 2100 under RCP 8.5 and BaU management scenario (Fig 6A). The same pattern was projected in Hereford Forest: the two species at risk occurring in this study area (Canada Warbler and Eastern Wood-pewee), were projected to not be sensitive to the vegetation changes in 2100 under RCP 8.5 and BaU scenario compared to the reference scenario (Fig 6C and 6D). However, Canada Warbler is predicted to largely increase in abundance by 2050 under RCP 8.5 and BaU management scenario compared to the reference scenario (Fig 6C).

The relative influence of the drivers of change showed a similar pattern under RCP 4.5 and RCP 8.5 in 2100 for Rusty Blackbird and Canada Warbler in both study areas (S5 Fig). For Eastern Wood-pewee, the climate-driven ecological processes were predicted to be more influential for a short period of time (before 2040) under RCP 4.5 while this influence should remain longer (up to 2070) under RCP 8.5 (S5 Fig). Moreover, for Eastern Wood-pewee and Rusty Blackbird, the magnitude of change was predicted to be greater under RCP 4.5 compared to RCP 8.5.

5. Best management measures for the dual-criteria approach

Moreau et al. [41] demonstrated that decreasing the level of forest harvesting had contrasting effects on the carbon emission mitigation potential of the forest sector in hemiboreal and boreal forest sectors, regardless of the climate change scenario. Hemiboreal landscapes were projected to be more vulnerable to climate change than boreal landscapes, and thus were predicted to become a net source of carbon over time. Scenarios projected to be best for carbon emission mitigation were not always optimal for avian conservation, depending on the region (Table 2). In the Montmorency Forest, relative to the BaU scenario, lower harvest rates increased carbon storage by preserving stands that remained important carbon sinks and limiting short-term emissions caused by harvest. Moreover, lower harvest rates reduced emissions from degradation of wood products during their service life and in landfills [41]. Similarly, these scenarios were projected to best maintain the regional bird diversity under climate change relative to the reference scenario (i.e., smallest change in bird abundance). In this context, increased conservation of this boreal forest landscape represents an optimal solution for

Table 2. Best possible management measures in a dual–criteria approach.

	Montmorency Forest		Hereford Forest	
	Best strategy	Dual-criteria objectives validated?	Best strategy	Dual-criteria objectives validated?
Birds	Conservation scenario	Yes, the conservation scenario was predicted to meet the 3 objectives: • Bird diversity conservation: Yes • Climate change mitigation: Yes	Strategies that reduce forest harvesting levels	No, compromises have to be made.
Carbon emission mitigation [41]	Strategies that reduce forest harvesting levels		Strategies that increase forest harvesting levels	

the conservation of bird diversity and the mitigation of carbon emissions. However, forest management intensity was projected to have opposite effects in the hemiboreal forest area. Indeed, in Hereford Forest, the decrease in forest harvesting level, relative to BaU, reduced the mitigation potential by increasing net carbon emissions; in this area, the growth and carbon sequestration potential of otherwise stagnating stands were stimulated by harvesting [41]. Yet, our results showed that such a strategy would result in much larger changes in bird assemblages than decreasing forest harvesting intensity.

Discussion

According to the simulations, a decrease in the level of forest harvesting could benefit bird conservation while also possibly contributing to climate change mitigation in the boreal forest study area, due to a reduction of carbon emissions from forest ecosystems and wood products [41]. However, it is important to recognize that such changes in management practices will have varied effects on different bird species. For instance, while some species that thrive in older, undisturbed forests may see population increases, others that depend on early successional habitats or mixed-age forests might experience reduced habitat suitability [85]. This underscores the complexity of forest ecosystems and the need for a nuanced approach to forest management that considers the diverse requirements of different species. In comparison, in the hemiboreal forest study area, strategies that increase forest harvesting levels could contribute to climate change mitigation by stimulating carbon sequestration in ecosystems, but they would have negative effects on bird conservation. Trade-offs would be thus necessary as the objectives of the dual objectives are not simultaneously accommodated. Furthermore, this study improves our understanding of how bird assemblages in the boreal and hemiboreal forests of eastern North America are likely to be differentially vulnerable to the combined effects of climate change and forest management. We found that the increase in deciduous vegetation resulting from both forest harvesting and climate change should favor bird assemblages associated with mixed and deciduous stands, to the detriment of assemblages associated with old-growth coniferous stands. Our simulations thus suggest an important future shift in the composition and abundance of boreal and hemiboreal bird assemblages. The magnitude of change was projected to be generally greater in more southerly hemiboreal forests than in boreal forests to the north. In addition, hemiboreal bird assemblages were projected to be mainly affected by climate change, whereas boreal bird assemblages were projected to be more affected by forest management. We estimated that 25% of the species in the hemiboreal forest study area and 6% in the boreal forest area are sensitive to climate change (defined as projected changes in abundance greater than 25%).

Contrasting effects in hemiboreal and boreal forests

Forest management and climate change were projected to have impacts on tree species composition in both boreal and hemiboreal forests. Yet, we detected contrasting agents of change

between the hemiboreal and boreal study areas, which then influenced bird abundances. In the simulations, climate change influenced stand-scale processes, such as tree growth and regeneration. In the absence of wildfire, forest inertia is high, leading to relatively low proportions of pioneer and deciduous vegetation in the boreal forest study area. This is in contrast with most of Quebec's boreal forest, where wildfires are a major disturbance and for which climate models suggest a strong increase in the upcoming decades [34, 86]. Such a climate-induced increase in wildfire would lead to an increase in pioneer and deciduous vegetation (e.g., trembling aspen) within younger naturally disturbed landscapes, resulting in a global northward expansion of temperate and hemiboreal at the expense of boreal forests [13]. The relatively small changes in vegetation observed in the boreal forest study area may be partly attributed by its higher elevation, which, while not mountainous, is higher than the surrounding lowland regions, ranging from approximately 600 to 1000 meters above sea level. This elevation, albeit moderate, may offer some degree of buffering against the more immediate impacts of climate change due to the cooler temperatures associated with increased altitude [24]. Therefore, within the current century, these factors could contribute to the limited climate-induced changes in forest composition and consequent subtle shifts in bird abundance projections locally [24, 87].

Larger climate-induced changes in forest composition were projected in the hemiboreal study area relative to the boreal study area. The Hereford Forest is located at the edge of the transition zone between temperate and hemiboreal forests, with many boreal tree species being near their southernmost range. Consequently, those mostly coniferous tree species coexist with more thermophilous deciduous species in a highly unstable and competitive ecosystem. Small variations in climatic conditions can thus result in changes in forest structure and composition [88] with pure conifer stands likely to be replaced by deciduous and mixed stands [89]. Accordingly, our simulations projected that bird species associated with boreal conifers, such as the Magnolia Warbler (*Setophaga magnolia*) and the Golden-crowned Kinglet (*Regulus satrapa*), would decrease, while species associated with deciduous forest, such as Baltimore Oriole (*Icterus galbula*) and the Warbling Vireo (*Vireo gilvus*) would increase under RCP 8.5. These changes in species composition are captured by an increase in the Shannon diversity index, which in our study is driven by variations in evenness rather than richness. Models consistently projected no change in bird species richness; thus, the observed increase in the Shannon index underscores a greater evenness in species abundances. Specifically, it reflects a shift towards a more balanced community, with deciduous-associated species becoming more prevalent and reducing the abundance of conifer-associated species, thereby increasing the evenness across the bird community. Our results are consistent with other studies suggesting climate-induced decreases in bird species associated with mature coniferous and mixedwood stands [25, 75]. The findings of our research indicate that hemiboreal forests, which are transitional zones between boreal and temperate forests, are likely to experience more pronounced changes in bird assemblage composition as a result of increased anthropogenic climate forcing, especially if these forests remain largely free of wildfires, as reflected in our boreal forest simulations. Furthermore, bird populations at the southern edge of their distributions—often referred to as 'trailing-edge' populations—are particularly at risk. These populations tend to be smaller, more isolated, and thus more susceptible to environmental disturbances compared to their counterparts in the central part of the range [90–92]. In addition, these trailing-edge populations may be exposed to increased competition and predation pressures from species that are expanding their range due to shifting climatic conditions [91].

In our boreal forest study area, bird assemblages were projected to be more strongly impacted by forest management compared to the hemiboreal forest study area, even though the projected percent change in bird abundance and the variations in the Shannon diversity

index remained low. In the boreal forest area, forest management is mainly based on clearcutting and will thus alter stand age by targeting older stands [93, 94]. This strategy favors species associated with young stands, such as Lincoln's Sparrow (*Melospiza lincolnii*), Mourning Warbler (*Geothlypis philadelphia*) and Wilson's Warbler (*Cardellina pusilla*). While mixed and coniferous stands are projected to persist, forest management involving higher harvested volume or shorter rotations may have important impacts on bird assemblages by removing mature stands with which many bird species are associated (i.e., Bay-breasted Warbler (*Setophaga castanea*), Brown Creeper (*Certhia Americana*) and Black-backed Woodpecker) [95, 96]. These results are also consistent with studies in both in eastern and western [21, 96, 97] boreal regions of North America, highlighting historical declines for bird species associated with coniferous and mixedwood forest types [98, 99].

In contrast, harvesting practices are exclusively partial cuts in the hemiboreal forest area. Accordingly, forest stands are thus predicted to conserve an uneven-aged structure including old cohorts, which favors the maintenance of species associated with mature forest stands. However, forest management was projected to exacerbate the impact of climate change in the hemiboreal area. For example, under RCP 8.5, deciduous forest-associated species like Warbling Vireo were projected to increase more under intensive forest management than under Business-as-usual (BaU) forest management. Similarly, conifer-associated species like Blue-headed Vireo were projected to decrease more under intensive forest management compared with the BaU forest management. Moreover, moderate disturbances are known to have favored the increase of warm-adapted species and have led to a broad-scale community thermophilization of forests at the hemiboreal–boreal ecotone in Québec in the last decades [35, 100]. Under a warming climate, moderate disturbances induced by partial cuts may similarly accelerate forest composition changes through more deciduous and mixed forest stands, consequently favoring associated bird assemblages. Finally, our study highlights the importance of forest landscape conditions (age structure, composition, etc.) at the beginning of the simulations, which were due to both natural disturbances and forest management histories. These starting conditions greatly influenced simulated successional trajectories. Indeed, the effects of historical disturbances on ecological communities may persist for decades to centuries [101]. The state of the initial ecosystem characteristics induced by past climate and disturbances may also partly explain our contrasting projections between boreal and hemiboreal ecosystems [35].

Contrasting impacts on bird assemblages between areas

Our projections highlighted great variations in bird abundance within regional assemblages, suggesting that novel species assemblages are likely to emerge [3, 102]. Due to differential multivariate habitat associations among species, trends in bird assemblages associated with a particular habitat class could be mixed. For example, in the hemiboreal area, Baltimore Oriole and Black-throated Blue Warbler are both species associated with closed deciduous stands. However, Baltimore Oriole would be favored by climate change and intensive forest management, while we projected an opposite effect for Black-throated Blue Warbler. At the assemblage level, we determined a global positive effect of climate change and intensive forest management for the assemblage of birds associated with closed deciduous stands. This contrasting effect between two bird species within the same assemblage highlights the importance of incorporating species-specific information to assess their relative risk of local or global extinction.

We also showed that drivers of change (i.e., climate change and forest management) are not projected to impact bird species equally across regions and time scales. Indeed, several species showed opposite trends between the boreal and the hemiboreal areas, as a response to climate- and forest management-induced changes on forest landscapes. As management strategies may

sometimes be based on species' rangewide trends, our projections highlighted the need to consider regional differences in projected bird assemblage change.

The consideration of threatened and non-threatened species is also crucial because of the spatial heterogeneity in bird responses. For instance, Canada Warbler is listed as Threatened in Canada because of steep long-term and large-scale population declines (Species at Risk Act, Schedule 1). At the regional scale, our projections suggested that Canada Warbler populations are better equipped to cope with the effect of changing climate than other non-threatened species, such as Black-throated Green Warbler and Blue-headed Vireo. The mismatch between historical trends and future projections could signal that non-breeding factors are driving declines [99, 103]. Conversely, bird species that are currently not considered at risk may be strongly impacted by the effects of climate change, and thus may require specific conservation measures before their situation becomes concerning. For instance, Northern Parula is classified as a least concern species [104], while our results projected a strong decline under RCP 8.5 and for all levels of forest management in the hemiboreal forest area (Mean percent change = -42%, S6B Table).

Limitations

Our projections are useful for identifying spatially heterogeneous responses to the cumulative impacts of climate change and forest management. Yet, our simulations focused on bird habitat responses (i.e., climate exposure), and did not consider species sensitivity or adaptive capacity, the other components of climate-change vulnerability [105]. Heterogeneous climate-change responses among co-occurring species may be based on different life history characteristics, such as life span, fecundity, or migration strategy. As such, our projections may have underestimated the impact of climate change on climate-sensitive species. Moreover, bird assemblages in this study were based on expert opinion and not on BRT results. We thus observed great variations in bird abundance changes within regional assemblages. Also, our projections did not account for potential new species expanding their range into the study area, notably from the south. The novel associations of species that have not co-evolved would result in new interactions and therefore could have negative impacts on the fitness of some species [29]. Additionally, the arrival of novel assemblages will challenge land managers to consider the functional value of this changing ecosystem. We considered scenarios to be beneficial for bird diversity when the percent change in bird abundance compared to the reference scenario was low. However, we did not consider functional diversity, which that can affect ecosystem resistance and resilience to disturbance [106, 107].

In addition, we only used outputs from the CanESM2 model to project the impacts of climate change on forest landscapes. This model is recognized as being on the warm and dry sides of the suite of global circulation and earth system models and so, our results must be interpreted in the light of these constraints. This choice was driven by previous simulations performed by Moreau et al. (2022) who projected carbon outputs used in this study. Further projections should consider an ensemble of different climate outputs to project future forest landscapes and bird habitats although such an endeavour would be computationally intensive.

Furthermore, it is crucial to consider both ecological and technical limitations. Indeed, the use of a 250-m resolution in our LANDIS-II simulations may not fully capture the fine-scale habitat complexities of forest ecosystems; especially in the hemiboreal region, where small, heterogeneous stands and uneven cutting systems prevail. This could introduce a degree of uncertainty in our projections that has not been fully characterized.

Finally, we recognize that our study does not compare the relative magnitude of ecological impacts against the broader backdrop of climate change mitigation (i.e., carbon balance).

Conservation thresholds are typically established at local and regional scales, reflecting the varied biodiversity conservation targets across regions. In contrast, climate-change thresholds are assessed on a more global scale. This dichotomy necessitates a multi-scale approach to risk assessment, integrating specific biodiversity targets and emission reduction goals. Such an approach would enable a balanced evaluation, considering both the localized ecological impacts and the broader context of climate change mitigation, facilitating informed decision-making for environmental management at various scales.

Acknowledging these limitations, future studies should aim to enhance model resolution and expand the empirical underpinnings of scenario-based projections. A balanced evaluation of the ecological and economic trade-offs at different scales is essential for informed decision-making in forest management, guiding strategies that judiciously weigh the benefits of climate change mitigation against the imperative of biodiversity conservation.

Implications for dual-objective forest management

We demonstrated spatial and temporal heterogeneity in the cumulative climate- and forest management impacts on hemiboreal and boreal bird assemblages. Moreau et al. [41] showed that the capacity of forest ecosystems to act as a carbon sink depended on the characteristics and dynamics of the vegetation that can be manipulated through forest management practices. These results call for efficient and regionally specific adaptive strategies [15, 32]. Yet, some broad recommendations emerge from this work. Specifically, decreasing forest harvesting rates in this region would have a positive impact on bird assemblages associated with mixed and coniferous forests in both boreal and hemiboreal forests. In boreal landscapes, lengthening cutting rotations and increasing the areas dedicated to partial cutting and conservation should help maintain coniferous species and older stands, even under high anthropogenic climate forcing. It could also potentially increase the reduction of carbon emissions through increased net carbon sequestration in forest ecosystems and reduced emissions from wood products. For instance, we showed the negative effects of an increase in forest harvesting on mature forest-associated species such as the Black-backed Woodpecker, Black-throated Green Warbler, Golden-crowned Kinglet, and Eastern Wood-pewee (the latter a species at risk). A lengthening of forest rotations and an increased use of partial cuts can also provide benefits in terms of long-term carbon storage in wood products by increasing the size of timber at the time of harvest, thereby generating higher-quality, longer-lived wood products [42]. Moreover, our results suggest that in the absence of wildfire, boreal forests are better equipped to retain current bird assemblages compared to hemiboreal forests in this region. Less moisture-limited than their western counterparts, eastern boreal forests may thus provide refugia from climate change for boreal birds.

The conservation of unharvested areas, such as in the conservation management scenario, may mitigate the negative effect of climate and forest management-induced habitat loss for some bird species. Indeed, when the availability of suitable habitat is low, the fragmentation of the forest would decrease the probability of bird occurrence for certain species, such as Ovenbird (*Seiurus aurocapilla*) [108] and American Three-toed Woodpecker (*Picoides dorsalis*) [109]. This is particularly important with the historical [110] and predicted future decline [71] in mature forest in eastern Canada. We expect that conservation management would also promote a diversity of wildlife habitats, and thus be beneficial for other local taxa, such as mammals (e.g., boreal caribou (*Rangifer tarandus caribou*)) and beetles [111]. The implementation of such practices (i.e., lengthening cutting rotations, increasing the areas dedicated to partial cutting, and maintaining large unharvested areas) is thus projected to have broader biodiversity benefits. Furthermore, other forest management practices could be implemented to help

restore or maintain specific habitats, for example with the manipulation of stand composition through selected cutting and planting; such practices are already routinely done by forest managers to ensure the quality of timber supply. However, as we demonstrated, species show heterogeneous responses to both climate and forest management. Thus, we urge caution in generalizing our results to other taxa or boreal regions.

As we showed, it is challenging to manage forests in the context of climate change and find strategies that benefit multiple ecosystem services and functions. Our study suggested that, in the boreal forest region, the implementation of conservation management, including a change in harvesting practices (e.g., partial cut instead of clearcut, lengthening of harvest rotations) and an overall reduction of harvest levels, may be a good opportunity to show that multiple objectives can be jointly met. Conversely, in the hemiboreal forest area, carbon and biodiversity objectives were not simultaneously accommodated. Indeed, strategies that decreased forest harvesting levels reduced carbon sequestration in forest ecosystems relative to the BaU, and thus reduced the carbon emission mitigation potential of the forest sector [41], but were projected to benefit most of bird species present within the forest. This suggests that trade-offs will be necessary in this area, through more innovative strategies, to improve both bird conservation and carbon emission mitigation. Indeed, for both study areas, an optimal scenario would likely include (1) intensive harvesting targeted at stagnating stands that have a high potential for future growth (thereby stimulating carbon sequestration and ensuring wood production); (2) preservation of specific forest areas with high biodiversity value; (3) and adapted/extensive harvesting practices over the rest of the landscape. This approach aligns with the principles of the triad model of forestry, which offers a framework for achieving such balance across the landscape [112, 113].

Our research demonstrates the utility of scenario evaluation through spatially explicit models in informing and guiding forest management and policy decisions [114]. The modeling approach used in this study, and in various other studies, provides a robust framework for anticipating the impacts of forestry practices on forest structure, composition, and wildlife [50, 115, 116] and can offer a decision support system at different scales. We recommend the adoption of such integrative modeling approaches by policymakers and forest managers to improve regionally adapted conservation efforts, enhance biodiversity, and ensure sustainable forest use.

Supporting information

S1 Text. Details of the forest landscapes simulations with LANDIS-II.
(DOCX)

S1 Table. Main habitats for the bird species included in the study. The R^2 of the Boosted Regression Trees (BRT) is also shown.
(XLSX)

S2 Table. Details of the variables we used to model the relative abundance of birds. The variables characterize the forest structure and composition at two spatial extents: the original value assigned to each 250-m cell ("local effect") and mean values at landscape scale (750-m) based on a Gaussian filter.
(XLSX)

S3 Table. Relative importance of vegetation and topography predictors in each bird species BRT model.
(XLSX)

S4 Table. a. Non-metric multidimensional scaling (NMDS) ordination results for Montmorency Forest. **b.** Non-metric multidimensional scaling (NMDS) ordination results for Hereford Forest.
(XLSX)

S5 Table. Projections of changes in bird community abundances. Results are represented for the four forest management scenarios under RCP 8.5 by 2100 (mean ± SE). The relative contributions of key components of change (climate change and forest management) are also presented as values of ω^2.
(XLSX)

S6 Table. a. Projections of changes in bird species abundances in Montmorency Forest. Results are represented for the four forest management scenarios under RCP 8.5 by 2100 (mean ± SE). The relative contributions of key components of change (climate change and forest management) are also presented as values of ω^2. **b.** Projections of changes in bird species abundances in Hereford Forest. Results are represented for the four forest management scenarios under RCP 8.5 by 2100 (mean ± SE). The relative contributions of key components of change (climate change and forest management) are also presented as values of ω^2.
(XLSX)

S1 Fig. Mean aboveground biomass for each land cover. a. trends and b. differences in the proportion of cover classes for each of the four forest harvesting scenarios under either the baseline, RCP 4.5 or RCP 8.5 climate scenario. balsam fir (ABIE.BAL), white spruce (PICE. GLA), black spruce (PICE.MAR), red maple (ACER.RUB), sugar maple (ACER.SAH), white birch (BETU.PAP), american beech (FAGU.GRA), red spruce (PICE.RUB), and trembling aspen (POPU.TRE).
(TIF)

S2 Fig. Trends in the mean age of forest stands. Results are represented for each of the four forest harvesting scenarios under either the baseline, RCP 4.5 or RCP 8.5 climate scenario.
(TIF)

S3 Fig. Proportion in land cover aboveground biomass. Trends in the proportion of cover classes for each of the four forest harvesting scenarios under either the baseline, RCP 4.5 or RCP 8.5 climate scenario. balsam fir (ABIE.BAL), white spruce (PICE.GLA), black spruce (PICE.MAR), sugar maple (ACER.SAH), american beech (FAGU.GRA), trembling aspen (POPU.TRE), and red spruce (PICE.RUB).
(TIF)

S4 Fig. The relative contribution of drivers of change. The relative contribution of drivers of change (climate change (yellow) and forest management (green)) as values of ω2 (mean), under RCP 4.5 and RCP 8.5 at year 2050 and 2100 relative to the change simulated under baseline climate scenario.
(TIF)

S5 Fig. Percent change in abundance of sensitive bird species. Results are represented under RCP 4.5 and RCP 8.5 by 2100 relative to the change simulated under the reference scenario (Baseline–BaU scenario) in Montmorency (top), and Hereford (bottom) Forests. The temporal trends of the relative contribution of drivers of change (climate change (yellow) and forest management (blue)) as values of ω^2 under RCP 4.5 and RCP 8.5 is also represented. Shaded area represents |%change| < 25%. Species indicated with an asterisk represented species at

risk. Bird abbreviations can be found in S1 Table.
(TIF)

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